DICOTYLEDONOUS WOOD FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA, II

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The present report is the second in a series describing the results of an investigation of an assemblage of woods from the Upper Cretaceous of central California. As reported in the first paper (Page, 1979), most of the fossil specimens were collected from three localities, considered to be Maastrichtian in age, situated in the foothills of the Mt. Diablo Range, west of the town of Patterson in Stanislaus County: locality 1 (Del Puerto Creek); locality 2a (Black Gulch); and locality 2b (an unnamed site near locality 2a). Pertinent information about these sites was presented in the earlier paper. Chmura (1973) places locality 1 stratigraphically above locality 2a; localities 2a and 2b are essentially time equivalent (Stein, pers. comm.).

In the present report, two additional localities are represented:

Locality 3. Cache Creek; R4W, T12N, Sec. 2, SE¼, Morgan Valley 15′ quadrangle.

Locality 4. ½ mile north of Pigeon Point, San Mateo County.

Locality 3 is an exposure of the Sites Formation along Cache Creek, in Yolo County on the western side of the Sacramento Valley. Douglas (1969) and Passagno (1974) consider the Sites Formation as Coniacian in age, but correlations based on Goudkoff's (1945) foraminiferal zones place the locality in the G-2 zone, or middle to late Turonian (Popenoe *et al.*, 1960). Locality 4 lies west of the Coast Ranges in an outcrop of the Pigeon Point Formation along the San Mateo County coast one-half mile north of Pigeon Point. Although numerous faults hamper stratigraphic work in this area, Hall *et al.* (1959) and Wentworth (1960 and pers. comm.) agree that the age of the formation is Campanian.

All thin sections described here are deposited in the California Academy of Sciences Geological Collections in San Francisco (CASG), and reference to these specimens is by accession number. The term "pore" is used in reference to the vessel as it appears in transverse section. The term "fiber" is used in its generic sense as defined in the *Multilingual Glossary of Terms Used in Wood Anatomy* (1964). Omission of an important feature in a description indicates that it was not possible to observe it due to poor preservation of the specimen. Growth rings are mentioned only if they are present, and pore frequency has been omitted because distortion of the grain in most specimens did not allow statistically significant measurements. In a general way the relative frequency can be inferred from the illustrations. The specimens are classified according to a system presented in the form of a synoptic key in the first paper of this series. The system is artificial and is merely a practical way to handle the structural patterns found among the fossil woods

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under study that can not, for reasons discussed at length, be assigned to modern genera or families. The characters used in the classification are those most likely to be preserved; hence, groupings are defined according to distribution of pores and of axial parenchyma, and to type of perforation plate and of intervessel pitting. With reference to distribution of axial parenchyma, the intent was to separate specimens that have paratracheal parenchyma from those that do not. It is, however, necessary to reserve a category for those in which no axial parenchyma could be observed. The notion of frequency was inadvertently interjected into the classification by the designation of an alternative (''sparse or absent'') to the categories ''parenchyma apotracheal only'' or ''paratracheal parenchyma present.'' For the sake of consistency, the word ''sparse'' should be removed from the synoptic key. Axial parenchyma cells, whatever their frequency, either are or are not associated with vessels. If the parenchyma cells are sparse and are consistently associated with vessels, they are considered paratracheal; if they are sparse and are not consistently associated with vessels, they are considered apotracheal. It should be mentioned that axial parenchyma cells are often difficult to recognize in sectioned (particularly in transversely sectioned) material. In fossilized woods the problems are more severe: such cells are often obscured by grain distortion; in transverse section they can be confused with fibers in which the secondary walls have been destroyed. Furthermore, mineral deposits within a cell may simulate the secondary thickening of fibers. Because of the difficulties in recognizing axial parenchyma in transverse section, it is important not to rely solely on such sections for determining its presence.

SYSTEMATIC DESCRIPTIONS

The first four specimens—CASG 60133, CASG 60420, CASG 60421, and CASG 60422—are classified in Group III. This group is characterized by mostly solitary pores and by perforation plates with fewer than 50 bars. Several specimens belonging to this group were described earlier (Page, 1979). CASG 60133 represents section B2 (parenchyma apotracheal, intervessel pits opposite), and CASG 60420, CASG 60421, and CASG 60422 represent section C (paratracheal parenchyma present).

CASG 60133 FIGURES 1–4.

MATERIAL. Branch 2.5 cm. in diameter.

Secondary xylem. Diffuse porous, the pores solitary, numerous, average radial diameter 86 μm. (70–99), average tangential diameter 96 μm. (86–116). Perforation plates scalariform, slightly oblique, with less than 10 widely spaced bars. Intervessel pits small, round, opposite; pits to ray cells oval to almost scalariform; pits to parenchyma oval; average vessel element length 681 μm. (580–812). Parenchyma

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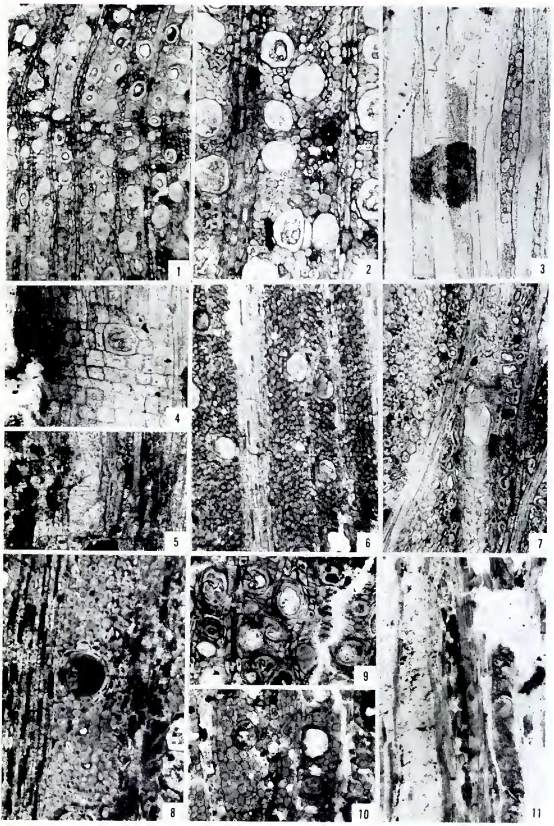
FIGURES 1–11. 1–4, CASG 60133: 1, transverse section (note growth ring), × 53; 2, transverse section, × 75; 3, tangential section, × 75; 4, radial section showing enlarged ray cell, × 75. 5–8, CASG 60420: 5, perforation plate, × 80; 6, transverse section, × 40; 7, tangential section (note broad rays and small intervessel pits), × 70; 8, transverse section, × 80. 9–11, CASG 60422, × 75: 9, 10, transverse sections showing pore distribution variants; 11, tangential section.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apotracheal diffuse. Rays 2 to 6 cells wide, numerous, the cells variable in size and shape, some much enlarged; uniseriates 1 to 6 cells high, heterocellular. Fiber pits on all walls small, bordered.

Pith. Large, 1 cm. in diameter; primary xylem points numerous, separated by multiseriate rays.

LOCALITY. Del Puerto Creek, locality 1.

Poor preservation obscured intervessel pits in all but a few vessels. Because of distortion, the uniseriate rays could not be counted; however, they do not seem to be numerous. Multiseriate rays are in various stages of dissection, and the lower rays have only one marginal row of square cells. Many are joined vertically by their uniseriate margins. The enlarged ray cells appear to have been crystalliferous (FIGURE 4). The pith is filled with convoluted, thick-walled tubules resembling hyphae of certain fungal pathogens.

Type IIB2 modern woods most similar to CASG 60133 include certain members of the Ericaceae, Escalloniaceae, Cunoniaceae, and Myricaceae. Solitary crystals have been reported in the Myricaceae (Metcalfe & Chalk, 1950).

CASG 60420 FIGURES 5–8.

MATERIAL. Fragment of mature secondary xylem.

Secondary xylem. Pores solitary, angular, some in radial pairs, average radial diameter 120 μm. (87–145), average tangential diameter 102 μm. (81–127). Perforation plates scalariform, 10 to 15 bars. Intervessel pits numerous, small to minute, opposite; pits to parenchyma similar, some elongated horizontally; average vessel element length 725 μm. (580–880); tyloses common. Parenchyma sparse, apotracheal diffuse and paratracheal as uniseriate sheath around some vessels. Multiseriate rays frequent, up to 15 cells wide and 2.7 mm. high, some dissected, the cells varying greatly in shape and size in no particular pattern, those in center mostly procumbent; uniseriates infrequent, 3 to 5 cells high. Fibers thick walled. Most elements containing dark, amorphous inclusions.

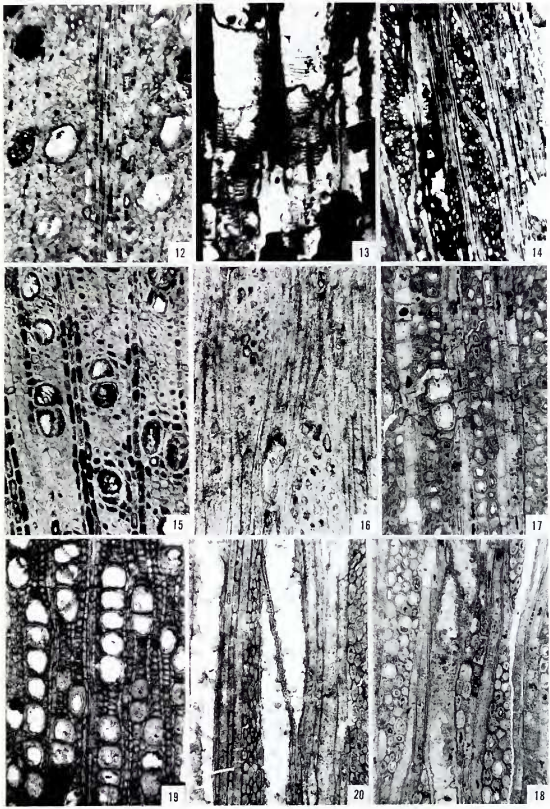
LOCALITY. Cache Creek, locality 3.

The amorphous inclusions and the tyloses obscure the end walls of many vessels; therefore, it is not certain whether all end walls are multiperforate.

Similar wood patterns can be observed in genera of the Araliaceae and Dilleniaceae. According to Dickison (1967), apotracheal parenchyma predominates in the Dilleniaceae, and paratracheal parenchyma is of a diffuse nature. Fibers are septate in most species of the Araliaceae. Although fiber septae were not observed in the fossil, their presence could be obscured by the amorphous inclusions in the very narrow cell lumens.

CASG 60421 FIGURES 12–14.

MATERIAL. Stem or root with what appears to be only secondary xylem, in one radial section with some evidence of primary xylem. Grain much distorted. Specimen probably from fork of a branch.



FIGURES 12–20. 12–14, CASG 60421: 12, transverse section, × 50; 13, longitudinal section showing wall pitting of ray and axial parenchyma cells, × 70; 14, tangential section, × 28. 15, 16, CASG 60423: 15, transverse section, × 40; 16, tangential section, × 70. 17, 18, CASG 60425: 17, transverse section, × 55; 18, tangential section, × 63. 19, 20, CASG 60424: 19, transverse section, × 42; 20, tangential section, × 70.

Secondary xylem. Pores solitary, angular, average radial diameter 139 μm. (102–203), average tangential diameter 171 μm. (87–232). Perforation plates scalariform, 40 to 50 bars. Intervessel pitting not observed; pits to ray cells and axial parenchyma scalariform or large and oval; average vessel element length 1413 μm. (1160–1624); tyloses common. Parenchyma paratracheal, apotracheal diffuse, and in uniseriate tangential lines. Rays up to 15 cells wide, averaging 1.7 mm. (1–2.7) high, heterocellular, the cells of central portion of large rays long procumbent, others short procumbent or square; uniseriate margins 1 to 5 cells high; sheath cells present; uniseriates numerous, up to 20 cells high, cells upright; rhomboidal crystals common. Fibers thick walled, the pits large, bordered, apertures small.

LOCALITY Del Puerto Creek, locality 1.

Similar wood patterns occur in *Dillenia* (Dilleniaceae), *Saurauia* (Saurauiaceae), and *Kaunbachia* (Cunoniaceae).

CASG 60422 FIGURES 9–11.

MATERIAL. Piece of secondary wood. Mostly compressed; grain distorted and cells crushed.

Secondary xylem. Observable pores solitary, differing in size and frequency in various areas of undamaged section where not compressed (difference possibly represents either various portions of growth ring or early- and later-formed wood), average radial diameter 86 μm. (58–104), average tangential diameter 78 μm. (58–93). Perforation plates scalariform, with ca. 15 coarse, widely spaced bars. Intervessel pits appear to be opposite, pits to ray cells and parenchyma scalariform; vessel elements ca. 770 μm. long; tyloses thick walled. Parenchyma appears to be mostly paratracheal. Rays 2 or 3 cells wide, the cells large, occasional larger ones may have been crystalliferous; sheath cells occasional; uniseriates appear to be infrequent. Fibers very thick walled, pit apertures small and slitlike.

Phloem. Patches of fibers alternating radially with enlarged thin-walled cells and crushed cells. Fibers small in diameter, thick walled. Large, thin-walled cells becoming stone cells in outer layers. Cells of rays not preserved, but no perceptible broadening of ray tissue in outer layers.

LOCALITY Del Puerto Creek, locality 1.

The next two specimens, CASG 60423 and CASG 60424, are classified in Group VA. Members of this group have scalariform perforation plates with fewer than 50 bars, both solitary and multiple pores, and little or no parenchyma. Examples of modern woods of this type with opposite and/or scalariform intervessel pits and with vessel elements that average more than 900 μm. in length include *Meliosma* (Sabiaceae), *Paypayrola* and *Leonia* (Violaceae), and several members of the Flacourtiaceae and Araliaceae. Those with opposite and/or scalariform intervessel pits and with vessel elements averaging less than 900 μm. in length include certain genera of the Staphyleaceae, Dichapetalaceae, Rhizophoraceae, and Araliaceae.

CASG 60423 FIGURES 15, 16.

MATERIAL. Small branch 4.5 cm. in diameter. Grain distorted.

Secondary xylem. Diffuse porous, pores solitary and in clusters and radial chains of 3 to 5, average radial diameter 98 μm. (58–128), average tangential diameter 81 μm. (46–104). Perforation plates scalariform, up to 18 coarse bars. Intervessel pits opposite, at least in part; pits to axial parenchyma large, oval; average vessel element length ca. 580 μm.; tyloses abundant. Parenchyma sparse, paratracheal. Rays 3 to 5 cells wide, over 1 mm. high, the cells large, mostly square or short procumbent; uniseriate margins 1 or 2 cells high, cells upright; uniseriates not numerous. Fibers septate in part.

Pith. Small, round; cells rounded, thin walled.

LOCALITY. Black Gulch, locality 2a.

The secondary xylem pattern is similar to some observed in the Araliaceae and the Rhizophoraceae. Fiber septae are difficult to find in the fossil, but some can be observed; since there is no evidence of fungal hyphae, it is reasonably certain that they are truly septae. The nature of the perforation plates is also difficult to discern in many vessels: many are unquestionably multiperforate, but it is possible that simple ones are also present.

This specimen is somewhat similar to CASG 60420, except that in CASG 60423 the rays are much narrower, no apotracheal parenchyma was observed, and pore multiples are present.

CASG 60424 FIGURES 19, 20.

MATERIAL. Small portion of mature secondary xylem.

Secondary xylem. Pores solitary and in radial rows of 3 to 5, average radial diameter 97 μm. (70–139), average tangential diameter 100 μm. (70–145). Perforation plates scalariform, bars averaging 35 (28 to 46). Intervessel pits small, opposite to laterally elongated; average vessel element length 1310 μm. (1160–1740). Parenchyma absent. Rays heterocellular, the cells mostly square, short procumbent, and upright, with some low procumbents; uniseriate margins 1 to 10 cells high, cells upright; many multiseriates connected vertically by margins; sheath cells occasional; uniseriates up to 14 cells high, cells upright. Fibers septate.

LOCALITY. Black Gulch, locality 2a.

Type VA woods, characterized by long vessel elements, opposite intervessel pits, and high heterocellular rays, occur in some of the more primitive members of the Violales. End walls in the vessels of the fossil have more bars than is characteristic of even the most primitive members of the Flacourtiaceae, and the intervessel pits are much smaller. There are numerous bars in the perforation plates in woods of the Violaceae, but intervessel pitting is scalariform or transitional. The family Lacistemaceae has small, opposite intervessel pits, but parenchyma in the four species examined is abundant.

Pollen attributable to the Lacistemaceae has been described from locality 1 (Chmura, 1973).

The next two specimens, CASG 60425 and CASG 60426, are classified in Group VB, which comprises woods with scalariform perforation plates with fewer than 50 bars, and pores both solitary and in multiples. Woods of this type occur in at least 23 families.

CASG 60425 FIGURES 17, 18.

MATERIAL. Stem or root 4 cm. in diameter.

Secondary xylem. Pores solitary and radially aligned in groups of 3 or 4, with some clusters, average radial diameter 93 μm. (72–114), average tangential diameter 81 μm. (64–107). Perforation plates scalariform, bars 10 to 15. Intervessel pits appear to be scalariform, average vessel element length 760 μm. (870–1100). Parenchyma abundant, apotracheal diffuse. Rays 2 to 4 cells wide, cells variable in size but mostly large and procumbent; uniseriate margins 1 or 2 cells high, cells square; uniseriates 3 to 10 cells high, the cells variable in size, mostly square.

LOCALITY. Del Puerto Creek, locality 1.

The wood anatomy of CASG 60425 is much like that of *Magnolioxylon panochensis*, a specimen described from locality 2a (Page, 1970), except that all the cells are larger, and the vessel elements are significantly shorter. CASG 60425 may represent a root or a stem of the same species or, since it was collected from a slightly younger locality, a different species altogether.

Few Group V woods have scalariform intervessel pits. Among those that do are *Hibbertia* (Dilleniaceae), and certain members of the Hamamelidaceae and the Magnoliaceae.

CASG 60426 FIGURES 21–23.

MATERIAL. Small stem 3 cm. in diameter.

Secondary xylem. Growth rings indistinct. Diffuse porous, pores solitary and in short chains and clusters, average radial diameter 58 μm. (46–80), average tangential diameter 46 μm. (40–58). Perforation plates scalariform, with up to 50 or more fine bars. Intervessel pits small, opposite transitional; pits to ray cells small, numerous; average vessel element length 748 μm. (580–870). Parenchyma abundant, apotracheal, diffuse and in tangential pairs. Rays numerous, uniseriate, up to 23 cells high, heterocellular. Fibers thick walled.

Pith. Small; cells small, rounded in transverse section.

Phloem. About 3 mm. thick, cells in no particular pattern, walls of parenchyma

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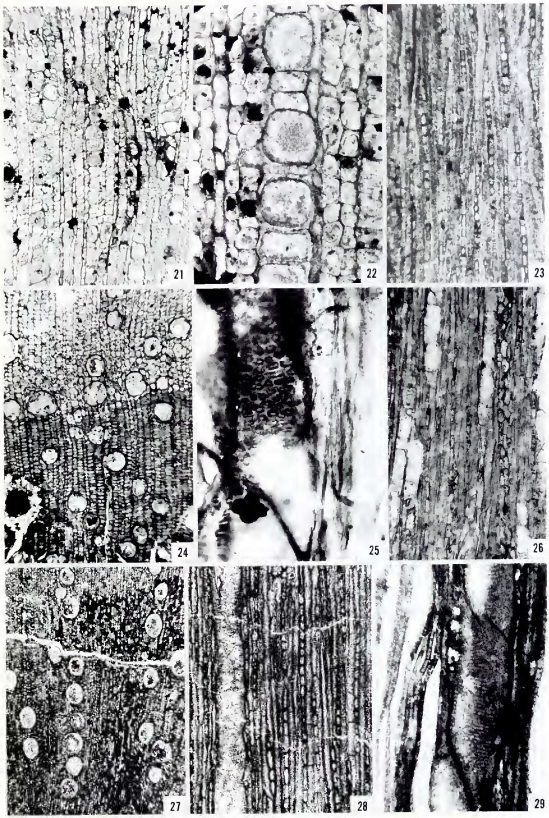
FIGURES 21–29. 21–23, CASG 60426: 21, transverse section, × 62; 22, transverse section, × 200; 23, tangential section, × 60. 24–26, CASG 60427: 24, transverse section, × 67; 25, longitudinal section showing bordered pits on vessel wall, × 250; 26, tangential section, × 60. 27, 28, CASG 60428: 27, transverse section, × 28; 28, tangential section, × 80. 29, CASG 60429, longitudinal section showing vessel wall pitting, × 70.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cells and ray cells highly thickened and tangentially elongated in outer layers. Rays continuous from xylem.

LOCALITY. Black Gulch, locality 2a.

Because preservation is poor, an accurate assessment of the number of end plate bars was not possible. It appears that most plates contain fewer than 50 bars; therefore, the fossil is placed in Group V.

Type VB woods, with vessel elements averaging less than 900 μm. in length, abundant parenchyma, and transitional to opposite intervessel pits, occur in such genera as *Ilex* (Aquifoliaceae), *Strombosia* (Olacaceae), and *Clethra* (Clethraceae). Except for its more numerous end plate bars, the fossil is similar to the wood of *Strombosia*.

Pollen attributable to both the Aquifoliaceae and the Olacaceae has been described from Black Gulch and Del Puerto Creek (Chmura, 1973).

The following specimen, CASG 60428, is classified in Group VIB. Members of this group have both simple and scalariform perforation plates, mostly solitary pores, and apotracheal parenchyma.

CASG 60428 FIGURES 27, 28.

MATERIAL. Small stem 3 cm. in diameter.

Secondary xylem. Pores ovoid, solitary, in slightly oblique arrangement, very small pores mixed with large ones, average radial diameter 121 μm. (70–153), average tangential diameter 104 μm. (87–157). Perforation plates simple and scalariform with up to 30 bars; intervessel pits alternate or slightly elongated horizontally, occasionally almost scalariform near pith; pits to ray cells similar, apertures coalescing obliquely in some cells; pits to parenchyma large; average vessel element length 551 μm. (406–696); tyloses occasional. Parenchyma abundant, apotracheal diffuse. Rays numerous, mostly uniseriate, some with biseriate centers, homogeneous to partly heterogeneous, up to 40 cells high, cells mostly procumbent, occasional marginal cells containing a single crystal. Fiber pits bordered; vasicentric tracheids occasional.

Pith. Cells large, thin walled.

Phloem. Alternating zones of fibers and stone cells separated by tangential rows of crushed thin-walled cells; cuboidal crystals occasional in parenchyma.

LOCALITY. Black Gulch, locality 2a.

Possibly because of poor preservation, vasicentric tracheids are discernible in only a few small areas in the two specimens with this pattern. All cells (except vessels) contain brown inclusions.

Patterns similar to the above occur in *Castanopsis* (Fagaceae), *Casuarina* (Casuarinaceae), and *Engelhardtia* (Juglandaceae). Abundant apotracheal parenchyma and an oblique arrangement of solitary pores form a common pattern in these families. According to Moseley (1948), no species of *Casuarina* has only diffuse axial

parenchyma. Although metatracheal bands of parenchyma are characteristic of most species of Juglandaceae and Fagaceae, there are some genera in which parenchyma is only diffuse. Vasicentric tracheids are characteristic of some genera of Fagaceae and at least one species of *Casuarina*. Scalariform perforation plates with few bars occur in species of some genera of the Juglandaceae including *Engelhardtia*, occasionally in small vessels in species of *Casuarina*, and in species of *Nothofagus* and *Fagus*. It is interesting to note that the three orders represented by these families are depicted by Cronquist (1968, p. 159) as closely related.

Pollen attributable to the Fagaceae and the Juglandaceae has been described from both Black Gulch and Del Puerto Creek (Chmura, 1973).

Group VIIC, which includes woods with both simple and scalariform perforation plates, pores in multiples as well as solitary, and some paratracheal parenchyma, is represented by specimen CASG 60427.

CASG 60427 FIGURES 24–26.

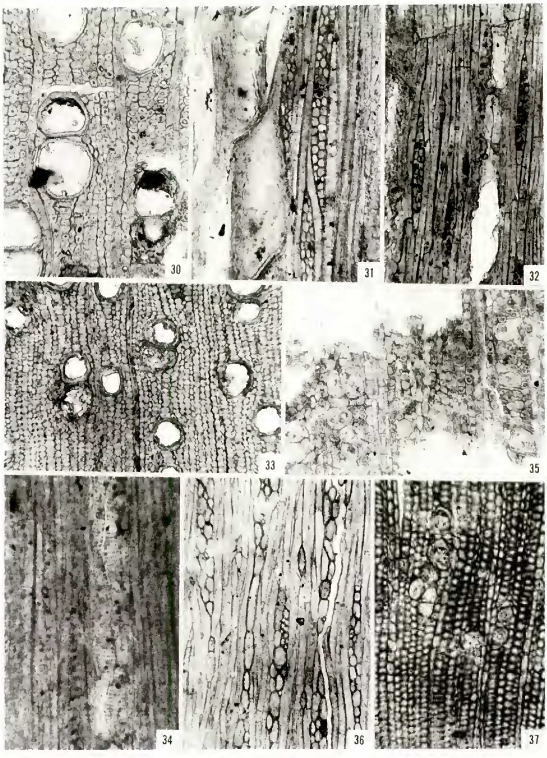
MATERIAL. Stem 2 cm. in diameter.

Secondary xylem. Semi-ring porous, the pores small, isodiametric, angular, solitary with some clusters and radial groups of 3, average radial diameter 49 μm. (43–58), average tangential diameter 52 μm. (35–70). Perforation plates simple, a few scalariform, usually with 3 or 4 bars. Intervessel pits scalariform and transitional to alternate, large, bordered; pits to axial parenchyma large, round, almost scalariform; average vessel element length 464 μm. (406–520); tyloses abundant. Parenchyma terminal and sparse paratracheal. Multiseriate rays infrequent, 3 cells wide, the cells upright, walls thick; uniseriates low, the cells upright, square. Fibers septate near vessels; long, narrow, scalariform-pitted, tracheidlike elements associated with some vessels.

Pith. Large, 7 mm. in diameter; cells small, more or less isodiametric, round in transverse section.

LOCALITY. Del Puerto Creek, locality 1.

Loss of material during preparation of the thin section destroyed portions of the single growth ring, and grain distortion obscures much of what remains. Most of the axial parenchyma is associated with the larger vessels at the inner edge of the outer ring. Because the ring is incomplete and distorted, it is impossible to be certain that what can be observed represents the normal structure of the stem. The scalariform pitting and abundant tyloses make it difficult to determine the nature of the end walls, although most appear to be simple. There is a progression from scalariform intervessel pitting to transitional alternate between the primary xylem and the outer portion of the stem, where a mixture of the two types occurs. The rays are of the kind generally considered juvenile. These factors indicate that the mature secondary xylem of the plant may have had wider multiseriate rays and a mixture of scalariform or transitional and alternate pits. Since the wood was in a state of transition, comparison with modern mature woods is valueless. All that can be said is that the fossil may be a transitional stage of mature patterns such as can be observed in some



FIGURES 30–37. 30, 31, CASG 60429: 30, transverse section, × 60; 31, tangential section, × 70. 32–34, CASG 60430: 32, tangential section, × 75; 33, transverse section, × 75; 34, longitudinal section showing vessel wall sculpturing, × 95. 35–37, CASG 60432: 35, transverse section near periphery of stem, × 75; 36, tangential section, × 73; 37, transverse section near pith, × 75.

Araliaceae and in *Leea* (Leeaceae): scalariform tracheids are characteristic of *Leea;* terminal or initial parenchyma is uncharacteristic of both *Leea* and the Araliaceae.

Group VIII is represented by specimens CASG 60429 and CASG 60430. Members of this group have simple perforations and scalariform, opposite, or transitional intervessel pits. This combination of characters is uncommon among modern woods but occurs in some Araliaceae, Cunoniaceae, Elaeocarpaceae, Fagaceae, Guttiferae, Leeaceae, Melastomataceae, Olacaceae, and Schisandraceae.

CASG 60429 FIGURES 29–31.

MATERIAL. Mature secondary wood.

Secondary xylem. Diffuse porous, the pores in multiples of 2 to 4, numerous, average radial diameter 143 μm. (100–174), average tangential diameter 110 μm. (75–156). Perforation plates simple, slightly oblique. Intervessel pits opposite, horizontally elongated to almost scalariform; pits to ray cells scalariform; average vessel element length 591 μm. (464–696). Parenchyma absent. Rays up to 3 cells wide, the cells mostly procumbent, varying in size; uniseriate margins 1 to 3 cells high, cells upright or square; uniseriates low, cells square or upright.

LOCALITY. Black Gulch, locality 2a.

Type VIII woods with little or no parenchyma have been observed in the Vitaceae, Melastomataceae, and Fagaceae (*Nothofagus*). According to Metcalfe and Chalk (1950), paratracheal parenchyma is always present in the wood of Melastomataceae and Vitaceae. Some Magnoliaceae have wood patterns similar to that of the fossil, but at least some vessels in these woods have scalariform perforations, and all have apotracheal parenchyma (mostly terminal).

CASG 60430 FIGURES 32–34.

MATERIAL. Secondary wood 2 cm. in diameter.

Secondary wood. Pores solitary and in radial rows of 2 to 4, rounded, but flattened in areas of contact, average radial diameter 69 μm. (52–81), average tangential diameter 64 μm. (46–75). Perforation plates simple. Intervessel pits scalariform; average vessel element length 350 μm. (286–394). Parenchyma apotracheal. Rays mostly 2 or 3 cells wide, averaging less than 500 μm. high, cells mostly procumbent; uniseriate margins 1 or 2 cells high; uniseriates infrequent, 1 to 9 cells high, cells square or upright.

LOCALITY. Locality 2b.

It is not certain that intervessel pits are scalariform in all vessels. Axial parenchyma is present, but it is not possible to determine its amount or distribution, except that no paratracheal parenchyma was noted. A very similar stem, CASG 60431, consisting of a pentagonal pith nearly 1 cm. in diameter surrounded by a layer of secondary xylem 13 mm. thick, was also collected at locality 2b. Near the pith there are a few scalariform perforation plates with four or fewer bars. The rays are higher

and more heterogeneous than are those in CASG 60430. The differences observed in the secondary wood of the two specimens are of the kinds that exist between early- and later-formed increments in the same plant.

Type VIIIB woods with diffuse apotracheal parenchyma occur in species of the Cunoniaceae, Fagaceae (*Nothofagus*), and Olacaceae.

Group IX, which includes woods with simple perforations, alternate intervessel pits, and no parenchyma, is represented by two specimens, CASG 60432 and CASG 60433. This pattern occurs in many families.

CASG 60432 FIGURES 35–37.

MATERIAL. Stem 4.5 cm. in diameter.

Secondary xylem. Pores solitary, in clusters, and in radial multiples of 3 to 6, average radial diameter 86 μm. (69–104), average tangential diameter 87 μm. (70–110), smallest near pith. Perforation plates simple, oblique. Intervessel pits alternate, crowded, minute; pits to ray cells similar; average vessel element length 301 μm. (261–406). Parenchyma absent. Rays numerous, 3 to 7 cells wide, heterocellular, the cells variable in size and shape, large, square, or short procumbent, very irregularly organized; sheath cells common; uniseriates infrequent, 1 to 4 cells high. Small elements resembling tracheids present (no perforations observed). Fibers very short.

LOCALITY Del Puerto Creek, locality 1.

It is difficult to determine whether the irregular ray structure was characteristic of the plant as a whole since the only specimen collected represents the fork of a branch. Because this irregularity is consistent in the many sections cut from the sizeable specimen, however, I assume that it is typical of the plant. It appears that many rays that are uniseriate in tangential section may be radial uniseriate extensions of multiseriate rays in the process of reduction in width. Preservation is poor, and the grain is often distorted; therefore, the total absence of parenchyma is not certain. It could not have been abundant, for it would surely have appeared in one of the sections. Some members of the Compositae and Solanaceae have similar woods.

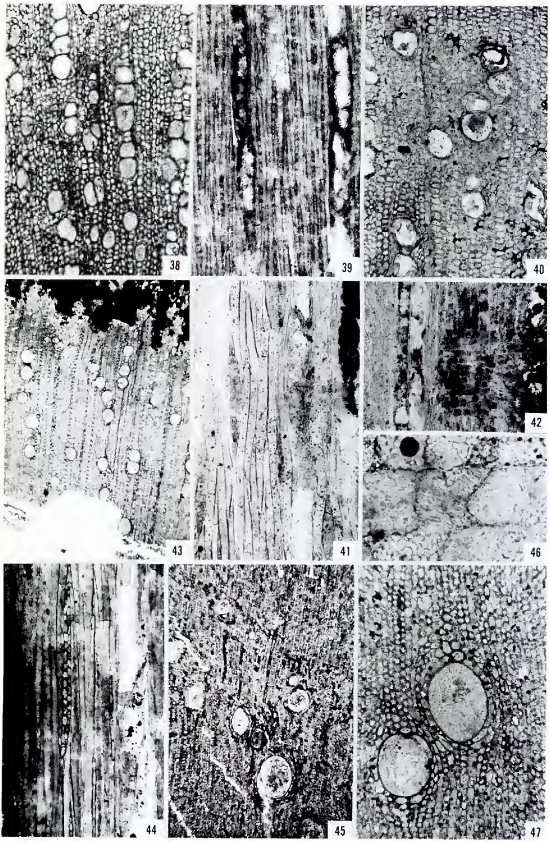
Pollen attributable to the Solanaceae has been described from locality 1 (Chmura, 1973).

CASG 60433 FIGURES 38, 39.

MATERIAL. Small stem 17 mm. in diameter.

Secondary xylem. Pores small, angular, mostly in radial multiples of 2 to 4,

FIGURES 38–47. 38, 39, CASG 60433, × 63; 38, transverse section; 39, tangential section. 40–42, CASG 60434; 40, transverse section, × 72; 41, tangential section, × 70; 42, radial section, × 70. 43, 44, CASG 60435; 43, transverse section, × 42; 44, tangential section, × 75. 45–47, CASG 60419; 45, transverse section, × 45; 46, radial section showing pitting on wall of ray cell, × 300; 47, transverse section, × 80.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clusters occasional, average radial diameter 69 μm. (34–87), average tangential diameter 50 μm. (29–58). Perforation plates simple, angle acute. Intervessel pits alternate, crowded, minute; average vessel element length 398 μm. (377–464). No parenchyma observed. Rays numerous, low, uniseriate, some biseriate, the cells small, square or short procumbent, some upright.

Pith. Almost 2 mm. in diameter; cells large, thin walled.

LOCALITY. Del Puerto Creek, locality 1.

Wood patterns similar to that of the fossil can be observed in certain members of the Euphorbiaceae, Moraceae, Punicaceae, Sonneratiaceae, and Rubiaceae.

Group XA, which includes woods with simple perforations, alternate intervessel pits, and diffuse apotracheal parenchyma, is represented by specimens CASG 60434, CASG 60435, and CASG 60419. Genera of many modern families are included in this group.

CASG 60434 FIGURES 40–42.

MATERIAL. Stem 2 cm. in diameter.

Secondary xylem. Growth rings apparent with magnification. Pores small, rounded, numerous, solitary and in radial pairs or triplets (occasional), average radial diameter 63 μm. (41–87), average tangential diameter 70 μm. (46–87). Perforation plates simple. Intervessel pits small, mostly alternate, some opposite, apertures sometimes horizontally elongated; vessel element length ca. 412 μm. Parenchyma sparse, apotracheal. Rays mostly low, average height 335 μm. (203–580), 1 to 3 cells wide, the cells square and short procumbent; uniseriate margins absent or up to 5 cells high, cells square or upright.

Pith. Small, round.

Phloem. Poorly preserved except for scattered stone cells and nests of fibers.

LOCALITY. Del Puerto Creek, locality 1.

Some fibers appear to be septate, but there is some doubt about this interpretation. In many fibers extremely fine fungal hyphae follow the contours of the inner wall, at intervals crossing the lumen and continuing along the wall in the opposite direction. Unless the cells are carefully examined, the hyphae can easily be mistaken for septae. It is possible that passage along the full length of the fiber was obstructed by septae, and that hyphae crossings thus actually indicate the presence of septae.

CASG 60435 FIGURES 43, 44.

MATERIAL. Stem 1.5 cm. in diameter.

Secondary xylem. Growth rings distinct, demarcated by tangential pore clusters. Pores mostly solitary, occasionally in clusters or radial files, average radial diameter 65 μm. (41–98), average tangential diameter 63 μm. (35–98). Perforation plates simple. Intervessel pits alternate, minute, the apertures narrow, extending beyond

borders; average vessel element length 423 μm. (3 measurements). Parenchyma apotracheal diffuse. Rays mostly biseriate, some 3 cells wide, up to 12 cells high, the cells small, square and short procumbent. Ground tissue mostly fibers, some with conspicuously bordered pits, mainly in vicinity of vessels.

Pith. Cells small, thick walled, round in transverse section.

Phloem. Groups of stone cells alternating with thin-walled cells; multiseriate rays flaring out and forming conspicuous wedges in outer portion; vertical files of "beaded" cells resembling chambered parenchyma, containing what appear to be remnants of polyhedral crystals.

LOCALITY. Del Puerto Creek, locality 1.

Due to poor preservation, the characteristics of the fibrous elements in the vicinity of vessels are not always clear. Those with conspicuous pits are not consistently associated with vessels.

The specimen is closely similar to *Carpinoxylon ostryopsoides* (Page, 1970). There are a few multiperforate vessels in *C. ostryopsoides*, the rays are wider, and the parenchyma is more abundant. Aggregate rays are also present. Among modern forms with aggregate rays, there is wide variation in the age at which these rays are initiated. Since CASG 60435 is half the diameter (3.0 cm.) of the specimen of *C. ostryopsoides* (mistakenly described as 1.5 cm.), and aggregate rays were observed in only the outer portion of the section, it is possible that these rays did not normally develop in early-formed wood. A specimen (CASG 60436) collected at an earlier date but from the same locality (2a) as *C. ostryopsoides* is quite similar, although it lacks aggregate rays. Close similarities were also observed in pith and bark among the three specimens, although only CASG 60435 has both tissues. *Carpinoxylon ostryopsoides* has a pith but no bark; CASG 60436 has bark but no pith. These two specimens are probably from the same kind of plant, while CASG 60435 may be a different species of either the same genus or a closely related one.

Although all three specimens compare favorably with the Coryleae of the Betulaceae (except for the smaller pits in the fossils), there are no modern genera that bear a close resemblance. There is some similarity to *Castanopsis* of the Fagaceae, but here the intervessel pits are also large, the vessel–ray pits are even larger, and the pores are exclusively solitary.

CASG 60419 FIGURES 45–47.

MATERIAL. Fragment of mature wood.

Secondary xylem. Pores solitary, rounded, ovoid, widely spaced in oblique radial arrangement, tangential clusters occasional, small pores mixed with large, average radial diameter 150 μm. (87–232), average tangential diameter 116 μm. (69–174). Perforation plates simple, horizontal or slightly oblique. Intervessel pits small, alternate, the apertures narrow, sometimes coalescent; pits to ray cells similar, apertures sometimes coalescing obliquely; average vessel element length 494 μm. (435–696); tyloses occasional. Parenchyma abundant, mostly apotracheal diffuse, but some paratracheal. Rays numerous, mostly uniseriate, up to 20 cells high, the cells

square, upright, or short procumbent; multiseriates infrequent, up to 4 cells wide, cells mostly procumbent; all ray cells containing dark brown substance. Fiber pits round, bordered, crowded.

LOCALITY ½ mile north of Pigeon Point, locality 4.

Axial parenchyma cells vary in diameter. It is sometimes difficult to distinguish between axial and ray parenchyma in radial section because the cells associated with vessels are small and frequently square or rhomboidal as in the rays. In transverse section, however, many large pores appear to have at least a partial sheath of parenchyma. Both rays and axial parenchyma are abundant; therefore, the association of either with vessels may be fortuitous.

There is a general similarity between this specimen and CASG 60428, but the cells in the rays of the latter are mostly procumbent, occasional cells contain crystals, and there is some evidence of vasicentric tracheids. Although scalariform perforation plates are present in CASG 60428, this may not be a significant difference since a stem collected at Black Gulch (CASG 60437) with secondary xylem identical to that of CASG 60419 has a few vessels with scalariform perforations in the early-formed wood.

CASG 60419 has many characteristics of some woods of the Myrtaceae and is also similar to *Licania* and *Parinaria* (Rosaceae), and *Monetes* and *Marquesia* (Dipterocarpaceae); however, some paratracheal parenchyma is typical of the latter two genera.

Group XIA is represented by 12 specimens consecutively numbered from CASG 60438 through CASG 60449. This group is distinguished by simple perforations, alternate intervessel pits, and vasicentric parenchyma—a pattern common among modern woods. A discussion of the relationship between the fossils and modern woods is presented following the descriptions of the specimens.

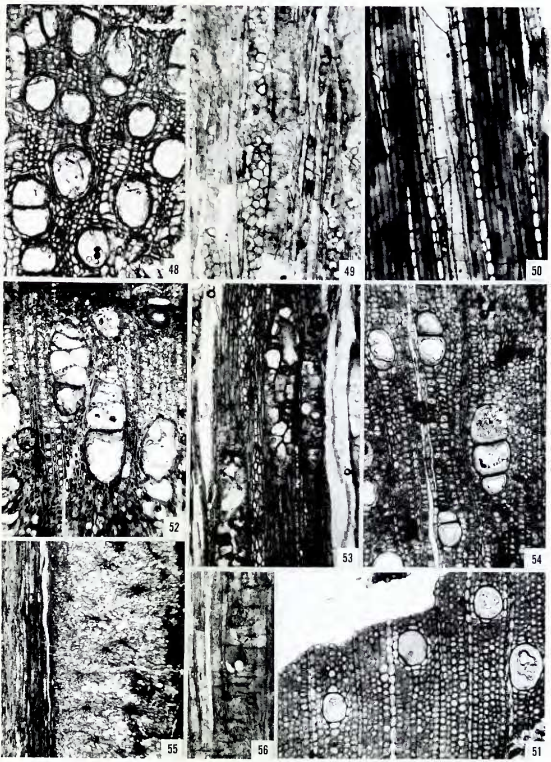
CASG 60438 FIGURES 48, 49.

MATERIAL An axis 2 cm. in diameter. The center is not preserved; therefore, it is not possible to determine whether the specimen is a stem or a root.

Secondary xylem. Pores large, solitary and in radial or tangential multiples of 3, average radial diameter 202 μm. (174–232), average tangential diameter 161 μm. (145–191). Perforation plates simple. Intervessel pits alternate, crowded, apertures narrow; pits to parenchyma large; average vessel element length 383 μm. (261–522). Parenchyma paratracheal. Rays 3 to 9 cells wide, up to 2 mm. high, the cells large, square or short procumbent; uniseriate margins lacking; uniseriates low, heterocellular; occasional cells with opaque, amber-colored inclusions. Fibers short, average length similar to that of vessel elements.

Phloem. Thick in proportion to amount of xylem; rays flaring out in cross section due to tangential expansion of cells; stone cells or other sclereids absent; many cells containing amber inclusions.

LOCALITY Del Puerto Creek, locality 1.



FIGURES 48–56. 48, 49, CASG 60438: 48, transverse section, × 38; 49, tangential section, × 54. 50, 51, CASG 60440, × 80: 50, tangential section; 51, transverse section. 52, 53, CASG 60439: 52, transverse section, × 38; 53, tangential section, × 24. 54–56, CASG 60442: 54, transverse section, × 70; 55, longitudinal section through pith showing nests of sclereids, × 6; 56, radial section showing enlarged secretory cell, × 85.

The large, numerous vessels and the high rays indicate that the plant may have been a liana. Inclusions such as those in the ray cells and bark may have been secretions of oil. The cells, however, are not especially enlarged. A proper radial section was not obtained.

CASG 60439 FIGURES 52, 53.

MATERIAL. Stem or root. Secondary xylem 1 cm. in diameter with bark 2.5 mm. thick.

Secondary xylem. There appear to be 13 or 14 faint growth rings. Pores large, solitary and in radial multiples, average radial diameter 232 μm. (128–365), average tangential diameter 174 μm. (116–232). Perforation plates simple. Intervessel pits small, alternate, apertures narrow; pits to rays variable, mostly large; pits to axial parenchyma large, oval; average vessel element length 548 μm. (464–638); tyloses abundant. Parenchyma paratracheal. Rays variable, some very high, 2 to 4 cells wide, heterocellular; uniseriates up to 6 cells high, cells variable; many cells containing amber-colored inclusions. Fibers short.

Phloem. Rays numerous, the cells enlarged tangentially, particularly at periphery of axis; scattered cells containing amber-colored inclusions; all cells thin walled, some parenchyma cells enlarged but lacking inclusions.

LOCALITY Del Puerto Creek, locality 1.

This specimen is somewhat similar to CASG 60438, although in that specimen the pores are more numerous, there are far fewer pore multiples, and tyloses are lacking. The presence of growth rings in CASG 60439 suggests that if it is a root, it may not have been subterranean.

CASG 60440 FIGURES 50, 51.

MATERIAL. Small stem 1.5 cm. in diameter.

Secondary xylem. Pores mostly solitary, some radial multiples of 2 to 4, slightly angular, average radial diameter 100 μm. (58–121), average tangential diameter 80 μm. (58–98). Perforation plates simple, slightly oblique. Intervessel pits large, crowded, alternate; pits to ray cells large, oval, irregularly oriented; average vessel element length 399 μm. (343–445). Parenchyma paratracheal, sheaths 1 or 2 cells thick. Rays mostly uniseriate, occasionally bi- or triseriate, the cells mostly square or upright, with numerous small pits on tangential and horizontal walls, occasionally slightly inflated and containing amber-colored inclusions. Some fibers septate.

Pith. 0.5 cm. in diameter; nests of sclereids numerous; protoxylem points numerous; pith cells in vicinity of primary xylem small, thick walled, other cells large.

LOCALITY Del Puerto Creek, locality 1.

A specimen (CASG 60441) collected at locality 2b and nearly identical in every way contains numerous inflated cells, which are interpreted to be secretory cells.

CASG 60442 FIGURES 54–56.

MATERIAL. Stem 22 mm. in diameter.

Secondary xylem. Pores solitary with occasional radial files of 2 to 5, average radial diameter 106 μm. (70–128), average tangential diameter 85 μm. (52-104). Perforation plates simple. Intervessel pits small, alternate, crowded, pits to ray cells large, oval; average vessel element length 365 μm. (290–435). Parenchyma sparse, paratracheal. Rays 1 to 3 cells wide, the cells short procumbent or upright, often enlarged and containing amber-colored inclusions.

Pith. Large, round; cells very large except in vicinity of primary xylem where small and thick walled. Nests of cells resembling potential sclereids common.

LOCALITY Black Gulch, locality 2a.

CASG 60443 FIGURES 57–59.

MATERIAL. Mature secondary wood.

Secondary xylem. Pores solitary and in occasional radial multiples of 2 to 4, rounded, average radial diameter 118 μm. (93–139), average tangential diameter 92 μm. (81–104). Perforation plates simple. Intervessel pits small, alternate; pits to ray cells large; length of vessel elements ca. 765 μm.; tyloses occasional. Parenchyma sparse, paratracheal. Multiseriate rays 4 or 5 cells wide, cells mostly procumbent; uniseriate margins 1 to 3 cells high, cells upright; uniseriates infrequent, 2 to 4 cells high, cells upright; rays widely spaced; some enlarged cells may have been crystalliferous. Fibers frequently septate.

LOCALITY Black Gulch, locality 2a.

CASG 60444

MATERIAL. Fragment of stem with pith and a small amount of secondary xylem.

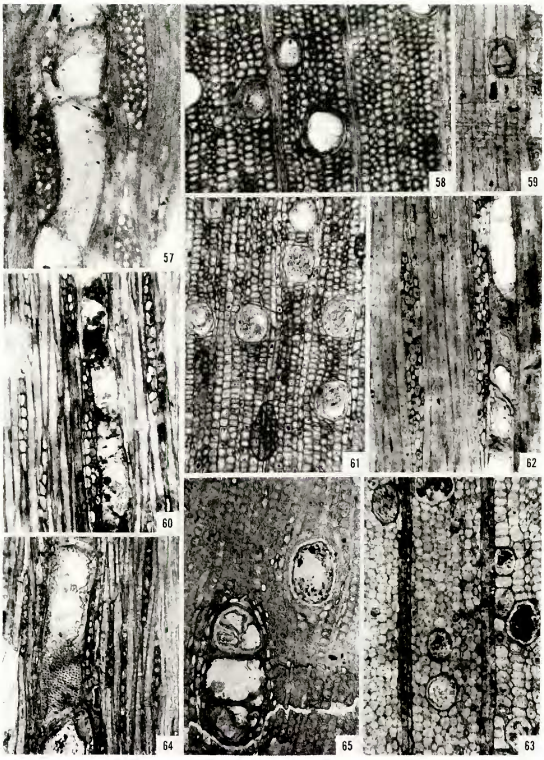
Secondary xylem. Pores mostly solitary and widely spaced with occasional radial multiples of 3, average radial diameter 129 μm. (104–174), average tangential diameter 115 μm. (93–145). Perforation plates simple, slightly oblique. Intervessel pits alternate, crowded; pits to parenchyma oval; length of vessel elements ca. 300 μm. Parenchyma paratracheal. Multiseriate rays mostly 3 cells wide, the cells mostly procumbent with 1 or 2 marginal rows of square cells, nearly homogeneous; uniseriates infrequent.

Pith. 1 cm. in diameter, with large, mostly peripheral cavities.

Primary xylem. Protoxylem points conspicuous, extending deep into pith, the adjacent pith cells very small, thick walled; average vessel diameter 79 μm. (63–93). Multiseriate rays extending into secondary xylem.

LOCALITY Del Puerto Creek, locality 1.

The nature of the peripheral pith cavities is difficult to determine. There is no structural evidence to indicate whether they were a functional part of the stem or



FIGURES 57–65. 57–59, CASG 60443: 57, tangential section, × 78; 58, transverse section, × 52; 59, radial section showing enlarged ray cell with contents resembling a crystal, × 80. 60, 61, CASG 60445: 60, tangential section, × 64; 61, transverse section, × 57. 62, 63, CASG 60448: 62, tangential section, × 78; 63, transverse section, × 70. 64, 65, CASG 60447: 64, tangential section (note small intervessel pits), × 78; 65, transverse section, × 75.

whether they were formed by some foreign agent. Vertical extent of the cavities is minimal.

CASG 60445 FIGURES 60, 61.

MATERIAL. Fragment of mature secondary wood, diameter 2.2 cm.

Secondary xylem. Diffuse porous, pores solitary with some radial pairs, radial files of 3, and occasional clusters of 3 or 4, average radial diameter 112 μm. (87–145), average tangential diameter 82 μm. (70–99). Perforation plates simple. Intervessel pits large, alternate; pits to ray cells large; vessel element length ca. 464 μm.; tyloses occasional. Parenchyma sparse, paratracheal. Rays up to 4 cells wide, irregular in height (0.58–3.1 mm.), some in process of dissection, the cells square and short procumbent, with tangential walls often inclined from vertical in radial section; uniseriate margins absent or up to 3 cells high, cells upright; uniseriates 1 to 4 cells high, cells variable in size and shape. Fibers thick walled.

LOCALITY. Locality 2b.

CASG 60446

MATERIAL. Small stem 1.5 cm. in diameter.

Secondary xylem. One distinct growth ring present. Pores mostly solitary, radial pairs numerous, clusters of 3 occasional, average radial diameter 88 μm. (73–102), average tangential diameter 80 μm. (58–102). Perforation plates simple. Intervessel pits alternate, fairly large, particularly in ligule; pits to ray cells large, oval; average vessel element length 406 μm. (348–464); tyloses abundant. Parenchyma sparse, paratracheal. Rays mostly 2 or 3 cells wide, cells of multiseriate portion mostly procumbent; uniseriate margins 1 to 5 cells high, the cells square or upright, uprights more common toward center of stem; uniseriates mostly 5 cells high, cells square; some cells containing dark globules.

Pith. Small.

Phloem. Appears to have checkered pattern of groups of thin- and thick-walled cells.

LOCALITY. Locality 2b.

CASG 60447 FIGURES 64, 65.

MATERIAL. Mature secondary xylem.

Secondary xylem. Pores mostly solitary with some radial multiples, average radial diameter 154 μm. (116–191), average tangential diameter 116 μm. (87–145). Perforation plates simple. Intervessel pits very small, alternate, apertures coalescent; pits to parenchyma oval; average vessel element length 407 μm. (314–515). Parenchyma paratracheal, sheaths 1 to 3 cells thick. Rays numerous, uniseriate or biseriate, 3 to 18 cells high, cells procumbent, some with one row of square cells at margins.

LOCALITY. Del Puerto Creek, locality 1.

CASG 60448 FIGURES 62, 63.

MATERIAL. Mature secondary wood.

Secondary xylem. Growth rings indistinct, defined by few rows of radially flattened fibers and somewhat smaller pores. Diffuse porous, pores mostly solitary or in radial pairs, average radial diameter 103 μm. (75–127), average tangential diameter 81 μm. (58–104). Perforation plates simple, angle acute. Intervessel pits alternate, large, apertures small; average vessel element length 412 μm. (406–580); tyloses thin walled. Parenchyma sparse, paratracheal. Multiseriate rays widely spaced, variable in height from 174 μm. to 1 mm., mostly 3 or 4 cells wide, cells low procumbent; uniseriate margins 1 to 3 cells high, cells square; uniseriates infrequent; all cells containing dark globules. Fibers large in diameter, average 29 μm.

LOCALITY Locality 2b.

CASG 60449

MATERIAL. Stem 2 cm. in diameter.

Secondary xylem. Pores solitary, in short radial files and in clusters, average radial diameter 52 μm. (29–75), average tangential diameter 53 μm. (29–81). Perforation plates simple. Intervessel pits not observed; pits to parenchyma large; average vessel element length ca. 500 μm.; tyloses abundant. Parenchyma paratracheal. Rays low (about 12 cells high), 2 (or 3) cells wide, cells square or short procumbent; uniseriates about 10 cells high, heterocellular. Fibers large in diameter, some septate.

Pith. 3 mm. in diameter, prominently 6-lobed in transverse section; cells small.

LOCALITY Del Puerto Creek, locality 1.

Except for its smaller pores and lower rays, CASG 60449 is very similar to CASG 60448. Since one would not expect to find higher rays in mature wood than in the juvenile wood of the same plant (see Bailey & Howard, 1941), it is unlikely that the two specimens represent the same natural species. The mature wood was collected from locality 2b, and the small stem from locality 1, a stratigraphic distance representing an estimated time interval of approximately one million years. Although there is a general similarity between these specimens and CASG 60430 and CASG 60434, no paratracheal parenchyma was observed in the latter two. In addition, intervessel pits in CASG 60430 appear to be scalariform, whereas those in CASG 60434 are opposite or alternate.

Among the many families with type XIA wood patterns, woods with little or no apotracheal parenchyma occur in at least eight. Special features, when present, serve to differentiate the various families. For example, secretory cells are characteristic of the Lauraceae, while radial canals and crystalliferous ray cells are found in the Anacardiaceae and Burseraceae. Canals also occur in the Araliaceae, and vestured intervessel pits are characteristic of the Leguminosae and the Combretaceae. Of the fifteen type XIA fossil woods described, CASG 60438, CASG 60439, CASG 60440, CASG 60442, and two specimens described earlier (*Ulminium pattersonensis* and *U. mulleri* (Page, 1967)) contain a few parenchyma cells that appear to have been oil or

secretory cells of some sort. In some specimens these cells are slightly inflated (FIGURE 56), but in others they are distinguished only by the presence of amber-colored inclusions. Pith sclereids such as those described in CASG 60442 and CASG 60440 occur in several members of the Lauraceae.

Infrequent rays, mostly solitary pores, and large vessel–ray pits as described in CASG 60443, CASG 60444, CASG 60445, and CASG 60446 are characteristic of families such as the Anacardiaceae, Burseraceae, and some genera of the Araliaceae. Crystalliferous cells (FIGURE 59) in the rays of CASG 60443 indicate a possible alliance with the Anacardiaceae and/or Burseraceae.

Pore multiples and low, numerous, mostly uniseriate rays composed of procumbent cells as described in CASG 60447 occur in some Combretaceae and Leguminosae. The presence of the vestured intervessel pits characteristic of these families is almost impossible to establish in fossil material.

There are no distinguishing features in CASG 60448 and CASG 60449; however, the six-lobed pith of the former is uncharacteristic of the Lauraceae.

CONCLUSIONS

Remains of leaves and pollen of Cretaceous angiosperms are sufficiently abundant to provide an adequate source of information for the study of pre-Cenozoic angiosperm history. By contrast, angiosperm wood is sparsely represented. Until the discovery of the suite of dicotyledonous woods from central California, only a few isolated specimens had been described. Very little, therefore, could be learned of the evolutionary history of the dicot stem. The number of specimens is still small, but we now have some evidence of the diversity of wood patterns that existed in the Upper Cretaceous, as well as some bases for observations with respect to the level of specialization displayed by these woods as compared with those described from later periods. Of special interest is the lack of highly specialized characters in the specimens of the collection studied. Such features have not been convincingly described in any other pre-Cenozoic woods of unquestioned provenance. There is, for example, no evidence of complex pore arrangements, storied elements, resin canals, or tile cells, and while axial parenchyma occurs in a variety of conditions, there is no evidence of multiseriate bands or aliform sheaths. Furthermore, there is a high proportion of specimens with scalariform perforation plates and medium or long vessel elements. The most highly specialized pattern is that of CASG 60432, which has infrequent uniseriate rays, highly disorganized multiseriate rays with the cells variable in size and shape, very short fibers, and no observable parenchyma. The wood, in fact, resembles the secondary xylem of certain members of the Compositae. Although a discussion of some of the above observations was presented in an earlier paper (Wolfe *et al.*, 1975), a more extensive treatment will be presented in a forthcoming report.

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